

Predation by Jaguar on Howler Monkeys (*Alouatta seniculus*) in Venezuela

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We document the loss of all but the youngest member of a troop of six howler monkeys due to probable jaguar predation during a 7-month period in 1988. The formation of Guri Lake resulted in forest fragmentation which forced monkeys into new and unfamiliar areas and altered the balance of predator and prey populations, and may thus have contributed indirectly to the success of the jaguar. The selection of defoliated (dead) trees for sleeping sites by the howlers may have directly increased the risk of predation. © 1992 Wiley-Liss, Inc.

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INTRODUCTION

The rate of predation on arboreal primates appears to be lower than on terrestrial primates [Anderson, 1986; Cheney & Wrangham, 1987], but the former are more vulnerable to raptors [Cheney & Wrangham, 1987]. Emmons [1987] found the remains of only six primates among 177 mammals represented in felid scat samples at Cocha Cashu, Peru. In contrast, primates comprised 41% of individual mammalian prey of harpy eagle (*Harpia harpyja*) in the Guyanas (15/27 [Fowler & Cope, 1964] and 30/83 [Rettig, 1978; Izor, 1985]), and harpy eagles have been observed to prey on *Alouatta* [Eason, 1989; Sherman, 1991]. The challenge of observing actual predation, together with its apparent low rate of occurrence, may explain why most reports of predation on primates are anecdotal. As pointed out by Isbell [1990: 50], "when the predator is a nocturnal, secretive felid that consumes most, or all, of its primate prey, direct observation of predation is virtually unobtainable even when predation rates are high."

We report the virtual elimination of a howler monkey (*Alouatta seniculus*) troop on an island in Guri Lake, eastern Venezuela. Physical findings (remains of dead howlers) and predator sightings during 4 months in 1988 provide evidence that the sequential loss of five adult howlers was due to the activity of a subadult or young adult jaguar (*Panthera onca*).

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METHODS

Guri Lake (Bolívar State, Venezuela) was formed as a consequence of flooding of the Rios Caroní and lower Paragua when a dam was built on the Caroní beginning in 1968. The final size of the lake (4,250 km²) was reached in November 1986, and resulted in the formation of more than 100 islands varying in size from less than 1 ha to more than 600 ha. The dam, the reservoir, and the land immediately surrounding the lake are under the administration of EDELCA (Electrificación del Caroní). The study group of howlers and a troop of white-faced sakis (*Pithecia pithecia*) inhabit one of five isolated forest patches interrupted by open savanna on a 70-ha island (Island I) near the north end of the lake (7°45' N, 62°52' W). Dead defoliated trees, standing in water, rim the perimeter of the island, but are most dense on the southern edge, extending 50 to 75 m into the water. A troop of *Cebus olivaceus* visited the study area occasionally. Larger, primarily forested islands are located within 1 km both to the north and the south of the study island. The native fauna is described in Alvarez et al. [1986]. Hunting is prohibited in areas administered by EDELCA, and has been successfully enforced on Island I.

The howler group of five adults plus a female juvenile was first observed during a survey of the island on May 30, 1988 [Kinzey et al., 1988]. Habituation and systematic study of the group began in August, and daily focal animal samples [Altmann, 1974] were conducted (by AP) during four observation periods from September 6, 1988, to March 23, 1990 (1: Sept. 6–30, 1988; 2: Oct. 29–Nov. 16, 1988; 3: June 26–Aug. 23, 1989; 4: Jan. 26–March 23, 1990). Ad libitum observations (including jaguar sightings and the finding of howler remains) were made from August through December 1988. In some cases of predation documented below, observers were present on the island undertaking other studies when remains were discovered.

The sole survivor of the troop is a juvenile, who was fully weaned at the onset of observations, but spent the majority of its resting time in contact with her mother [Peetz, 1990]. This individual, now a subadult, was still alive in January 1992.

RESULTS

The sequence of disappearances and physical findings are summarized in Table 1. We did not find evidence of the first adult, which disappeared between May 30 and August 20, although we suspect it was lost in the same manner as the subsequent four animals. In case 2 we found a substantial portion of the carcass. We probably disturbed the predator inadvertently since we located the remains in the morning, within 8 h of hearing the scream of a howler monkey at midnight. Jaguars do abandon parts of their prey [Schaller & Vasconcelos, 1978]. The puncture wounds found at the base of the back of the head of this mature male were characteristic of jaguar predation [Mondolfi & Hoogesteijn, 1986]. In the remaining cases (3–5), we found only fragmentary skeletal remains and/or hair. For cases 3 and 4, the date each animal was missing was known within 4 and 2 days respectively, but remains of hair were not found until later.

If the howlers recognized an increased threat of predation, they may have countered this risk by altering their activity pattern or changing location of sleeping sites. We therefore compared the location and distribution of trees used for sleeping at night and for resting during the day.

The howlers settled into sleeping trees late in the day, at or after dusk. All remains were found within 30 m of the south edge of the island and can be linked to the location of sleeping trees. The major behavioral difference found throughout

TABLE I. Sequence of Individuals Lost From a Troop of *Alouatta seniculus* in Guri, Venezuela, in 1988

No.	Dates			Sex	Age	Comments
	Missing	Remains recovered	Days after full moon			
1.	Unknown	—	?	?	adult	disappearance ¹
2.	Sept. 2	Sept. 3	+6	M	adult	body found nearly intact ²
3.	Oct. 16–19	Nov. 6	–6–9	F	adult	hair, fragmentary mandible ³
4.	Oct. 27–28	Nov. 15	+2–3	M	adult	hair and blood only ⁴
5.	Dec. 23	Dec. 24	+1	F	young adult	hair only ⁵

¹Animal was seen in group during survey on May 30, 1988, but missing when group was next seen on August 20, 1988.

²Fully adult male with lingual wear on premolars and molars and wear on the upper central incisors; puncture marks (4–5 mm in diameter) visible in occipital region of the head and back of neck; body intact with exception of two or three lumbar vertebrae, right femur, and right os coxae; peritoneal cavity opened from right side and intestines punctured; remaining internal organs appeared to be intact; deep laceration on ventral surface of prehensile tail; the body had been dragged about 4 m away from the base of a tree.

³Young, but fully adult female; mother of weaned infant; fragmentary mandible was broken on the corpus just posterior to the tooth row; both ascending rami missing; M3s in occlusion; minimal tooth wear. Note: size of canines and mandible suggested that these remains were those of the female 3 and not the large adult male (4).

⁴Adult male, visually estimated to be approximately twice the size of male 2. Only hair with scant blood recovered.

⁵Young female (small adult or subadult). Only hair recovered 1 day after reported missing.

the four periods of focal animal samples was a marked decrease in the number of sleeping trees along the southern perimeter of the island. Compare distribution of sleeping trees in Figure 1a and b (during periods when the predator was active) with Figure 1c and d (0.5–1.5 years later). In contrast, time of entering a sleeping tree did not vary, there were no seasonal differences in the distribution of sleeping trees, and trees used for diurnal resting periods remained well dispersed throughout the forest patch during all observation periods (Fig. 1).

During the first sampling period (September 6–30, 1988), immediately after loss of the second animal, the howlers slept in five dead (completely defoliated) trees still standing in water (67% of nights) and in three trees located at the water's edge (33% of nights) (N = 18) [Peetz, 1990] (Fig. 1a). In contrast, all resting trees were fully foliated live trees and only rarely located in the water.

Two more adults were killed by the beginning of the second observation period, when we observed only the young adult female and an infant. These two monkeys markedly reduced the number of nights they slept in dead trees standing in water (5/18 or 28%), but continued to sleep in trees along the south edge of the island (Fig. 1b). The young adult female was killed after the second observation period, and the juvenile female (now a subadult) was the sole surviving troop member during the third and fourth observation periods in 1989 and 1990. The juvenile slept in a tree in the water only once (out of nine nights) during the third observation period and did not sleep in the same tree twice (Fig. 1c). By the fourth observation period, the choice of sleeping trees had changed again, and she slept in the same tree on 4/9 nights (44%) and used five other sleeping trees only once. During this period none of the sleeping trees was defoliated or standing in water (Fig. 1d).

Felids were seen on three occasions, either in the forest or in the narrow beach-and-grass area between the water and northwest edge of the forest. The first sighting was a jaguarundi (*Felis yagouaroundi*) at dusk, but the other two were sightings of a small, probably young, jaguar (October 29: midday—disturbed while

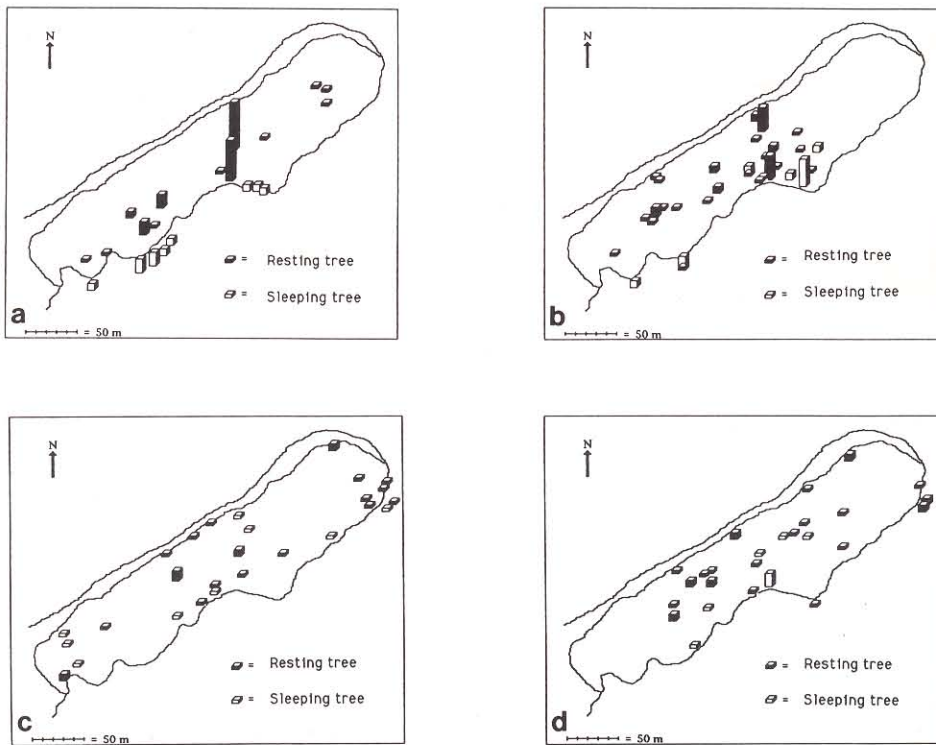


Fig. 1. Locations of howler sleeping trees and resting trees on Island I, Guri, Venezuela, during (a) first observation period—September 6 to 30, 1988 [adult male, adult female, young adult female, juvenile female]; (b) second observation period—October 29 to November 16, 1988 [juvenile and young adult females]; (c) third observation period—June 26 to August 23, 1989 [juvenile female]; (d) fourth observation period—January 26 to March 23, 1990 [juvenile female]. The height of each block represents the number of nights each sleeping tree was slept in (open blocks), or the number of times a resting tree was used (closed blocks) during the observation period. The outer line on the figure represents the perimeter of the island, the inner line on the northern edge represents the border of forest with beach. (No beach was present on the southern perimeter.)

resting in high grass on the northwest edge of the island; November 28: late afternoon—in the forest). On all three occasions, the cats moved rapidly into heavy undergrowth and could not be followed.

DISCUSSION

Strong circumstantial evidence suggests that the howler monkeys were victims of nocturnal predation by a young jaguar. The body weight of adult howler monkeys (4 to 10 kg [Crockett & Eisenberg, 1987:54]) is well within the range of jaguar prey. Even though jaguars are known to climb trees [Mondolfi & Hoogesteijn, 1986], arboreal mammals represent only a small portion of mammalian prey in their diet [Rabinowitz & Nottingham, 1986; Emmons, 1987]. Ocelots hunt terrestrially [Emmons, 1987], jaguarundi are too small to prey on adult howlers, and puma have not been seen in the area. The only previous evidence of predation on *Alouatta* by jaguar was the report of skeletal remains in a jaguar den [Mondolfi & Hoogesteijn, 1986].

The howlers would have been highly visible across open water from the large island to the southeast when they were sleeping in dead trees at the edge of the

island. The dead trees may have been traditional howler sleeping trees prior to the flooding. Howlers normally sleep on the horizontal branches of medium to large trees [Neville et al., 1988], although howlers also sleep in leafless trees in the llanos during the dry season [Crockett, pers. comm.]. Three of the known deaths occurred within 6 days after a full moon (Table 1), and although moonlight may hinder ocelot predation [Emmons et al., 1989], it may well have aided the jaguar.

If sleeping in defoliated trees improved predator visibility of prey, it is clear that the howlers did not respond immediately and unequivocally to the threat of predation. Increased vulnerability to predators may also have resulted from reluctance of troop leaders to give up traditional sleeping trees, and/or from movement by the monkeys into new and unfamiliar areas [Isbell et al., 1990] as when the lake was formed.

In what seems to be the only direct observation of felid predation of monkeys in trees at night, Busse [1980] described six leopard attacks on sleeping baboons in Botswana. Three baboons were killed—all adults. At the Botswana site both lion and leopard attacks were selective on adults. In our study, the first four howlers killed were adults and the fifth was a young adult. Of the original troop of six, only the juvenile survived. Thus, limited evidence suggests that predation by large felids on arboreal primates is selective for adults.

CONCLUSIONS

1. Strong circumstantial evidence suggests that four adult howler monkeys, and possibly a fifth, all from a single troop of six, were victims of nocturnal predation by a young jaguar during a 4 to 7-month period in 1988.
2. Predation involved an unusual series of events, precipitated by damming of the Caroni River and subsequent forest fragmentation from flooding of Guri Lake.

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